METABOLIC TYPES AND GROWTH TYPES

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The problem of the relation between metabolism and body size is one of the classical topics of physiology. It is usually treated in terms of the surface rule, established by Rubner in 1883, and heralded by earlier work of Sarrus and Rameaux, Bergmann and Richet. The surface rule states that the metabolic rate per unit weight decreases with increasing size, but is constant per unit surface. Rubner explained the surface rule in terms of homeothermy: Since all warm-blooded animals heat their bodies to a temperature of approximately 37°C, and since heat output takes place on the body surface, the same number of calories must be produced per unit surface. Even in recent discussions (Brody, 1945; Kleiber, 1947; Krebs, 1950) homeothermic animals are taken almost solely into consideration. It is necessary, however, to consider the problem on the broader basis of comparative physiology.

Such investigation has been carried through by the author and his co-workers (Bertalanffy, 1942 et seq.). The main results of this re-examination of the problem are:

(1) Recent investigation shows that the surface rule also holds for poikilothermic vertebrates and certain invertebrates. The rule as such is of a wide application, but current explanations, especially the explanation based on homeothermy, are too restricted.

(2) On the other hand, there are many classes of animals for which the surface rule does not apply.

(3) Thus we came to the statement of several metabolic types in respect to the relation between metabolic rate and body size. So far, three metabolic types have been distinguished.

In the first type, metabolic rate is proportional to a surface or to the \( \frac{3}{4} \) power of weight. Representatives of this type are fish, but also certain invertebrates, such as isopod crustaceans, according to our own investigations (Bertalanffy and Müller, 1943c), mussels (Weinland, 1919; Ludwig and Krywienczyk, 1950), and Ascaris (Krüger, 1940). As an example, metabolic rates in the sow bug, Armadillidium, are presented in table 1. The rate of oxygen consumption decreases per unit weight, but is constant per unit surface, expressed as the \( \frac{3}{4} \) power of weight. The most important question is, of course, whether the surface rule applies to mammals. This

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CO₂ PRODUCTION OF ARMADILLIDIUM PALLASII

(21°, mean values of 55 determinations)

<table>
<thead>
<tr>
<th>weight in mg</th>
<th>15</th>
<th>33</th>
<th>50</th>
<th>100</th>
<th>160</th>
</tr>
</thead>
<tbody>
<tr>
<td>cm³ O₂/h</td>
<td>3,0</td>
<td>5,2</td>
<td>7,2</td>
<td>11,2</td>
<td>15,2</td>
</tr>
<tr>
<td>per gm/h</td>
<td>200</td>
<td>174</td>
<td>144</td>
<td>112</td>
<td>94</td>
</tr>
<tr>
<td>per unit surface (W²A)/h</td>
<td>48,5</td>
<td>54,2</td>
<td>53,0</td>
<td>49,8</td>
<td>51,6</td>
</tr>
</tbody>
</table>

The question has been much discussed in recent years (Brody, 1945; Kleiber, 1947). In our work, the surface rule appears to be valid in the rat, comparing metabolic rates in individuals of different size (unpublished).

The second type is entirely different. Here metabolic rate is directly proportional to weight. The most important cases are insect larvae (Bertalanffy and Müller, 1943a; Teissier, 1931), and insects in interspecific comparison (Kittel, 1941), but equally hemimetabolic insects (Bertalanffy and Müller, 1943b) belong to this type. The example given is the walking stick, Dixippus morosus. Table 2 shows the constancy of metabolic rates per unit weight. Also land snails of the order Helicidae (intraspecific comparison: Bertalanffy and Müller, 1943a; interspecific comparison: Liebsch, 1929), and annelids, such as the earth worm (Bertalanffy and Müller, 1943c) belong to this type.

TABLE 2

OXYGEN CONSUMPTION OF DIXIPPUS MOROSUS

(20°, mean values of 20 determinations)

<table>
<thead>
<tr>
<th>weight in mg</th>
<th>8</th>
<th>130</th>
<th>250</th>
<th>450</th>
<th>630</th>
<th>850</th>
</tr>
</thead>
<tbody>
<tr>
<td>cm³ O₂/h</td>
<td>2,0</td>
<td>30,6</td>
<td>60,7</td>
<td>113,2</td>
<td>154,8</td>
<td>206,6</td>
</tr>
<tr>
<td>per gm/h</td>
<td>250</td>
<td>236</td>
<td>243</td>
<td>252</td>
<td>245</td>
<td>242</td>
</tr>
</tbody>
</table>

In the third type, metabolic rate is intermediate between weight proportionality and proportionality to surface. To this type belong pond snails such as Planorbus and Limnaea, and Planarians (Bertalanffy and Müller, 1943a). Table 3 demonstrates that metabolic rates decrease with respect to weight, but increase with respect to surface.

Now just as there are different types of metabolism, there are also different types of growth. The most common type of animal growth is that growth rates continually decrease with time and finally the organism reaches

TABLE 3

OXYGEN CONSUMPTION OF PLANORBIS SPEC.

(23°, mean values of 48 determinations)

<table>
<thead>
<tr>
<th>weight in mg</th>
<th>30-35</th>
<th>58-62</th>
<th>90-100</th>
<th>140</th>
<th>190-200</th>
</tr>
</thead>
<tbody>
<tr>
<td>cm³ O₂/h</td>
<td>2,3</td>
<td>3,9</td>
<td>5,4</td>
<td>7,3</td>
<td>9,5</td>
</tr>
<tr>
<td>per gm/h</td>
<td>69</td>
<td>65</td>
<td>56</td>
<td>52</td>
<td>48</td>
</tr>
<tr>
<td>per unit surface (W²A)/h</td>
<td>22,9</td>
<td>25,1</td>
<td>26,1</td>
<td>27,0</td>
<td>28,2</td>
</tr>
</tbody>
</table>
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FIGURE 1. (a) Respiration at 20°C (mean values of 85 determinations); (b) growth curves in the fish, Lebistes reticulatus. Calculation of linear growth: \( \text{---} \); of weight growth: \( \text{---} \). Equation for linear growth:

\[
x = X - (X - x_o)e^{-kt},
\]

for weight growth:

\[
y = \left[\sqrt[3]{Y} - \left(\sqrt[3]{Y} - \sqrt[3]{y_o}\right)\right]e^{-kt}.
\]

\(x, y\) = length, weight at time \(t\); \(X, x_o, Y, y_o\) = final and initial length and weight, respectively; \(k = \kappa/3\).

A steady state in the adult. There are, however, also other types of animal growth. It appears that it is possible to establish a strict connection between growth types and metabolic types with respect to the dependence of metabolic rate on body size. We give typical examples for these types.

In the first type, metabolism is surface-proportional. Figure 1 shows metabolism and growth in the guppy, Lebistes reticulatus. Metabolic rates are presented in allometric or log-log plot against weight. In the case of surface proportionality, the allometric line has a slope of \(\kappa\). The corresponding growth curve of this type is characterized as follows: (1) Growth rates are decreasing and the growth process attains a steady state; (2) the curves of growth by weight and linear growth show characteristic differences: the curve of weight growth has a point of inflection at about \(\kappa\) of the final weight, the curve of linear growth shows simple exponential decrease.
As an example of the second type, we give metabolism and growth in insect larvae (figure 2). In this type, metabolic rate is weight-proportional and therefore gives an allometric line of slope 1. Growth is here exponential, that is, growth rates always increase and no steady state is reached. Growth is only intercepted by a sort of crisis which is represented by metamorphosis in insect larvae, by seasonal cycles in land snails, which, as said before, also belong to this type.

In the third type, metabolic rate stands between proportionality to weight and proportionality to surface, giving an allometric line of a slope between ½ and 1. Our example is the pond snail, Planorbis (figure 3). In this case the curve of weight growth does not differ much from that of the first type, but the curve of linear growth is characteristic. While in the first type the curve has no point of inflection, it has one in the third type.
The relation between metabolic types and growth types can be explained, and many surprising predictions can be made on the basis of a theory on animal growth advocated by the author (1941, 1942, 1948, 1949). Growth is considered to be the result of a counteraction of anabolism and catabolism of building materials, according to the following basic expression:

$$\frac{dy}{dt} = \eta y^m - \kappa y^n.$$  

In words: the change of body weight \( y \) is given by the difference between the processes of building up and breaking down: \( \eta \) and \( \kappa \) are constants of anabolism and catabolism respectively, while the exponents \( m \) and \( n \) indicate that the latter are proportional to some powers of body weight \( y \).

Catabolism is, at least in a first approximation, proportional to weight so that the exponent \( m \) can be set equal to 1. Inserting for the exponent of anabolism \( m \) that value which is found for size dependence of metabolism, the types of growth automatically follow and the formulas for laws governing the several growth types can be deduced. The mathematical formulations are given elsewhere (Bertalanffy, 1941, 1942). It can be said, however, that these deductions have been found valid in all cases sufficiently investigated. Ludwig (1950) who is one of the most active workers in this field in Continental Europe, states that "no contradictions were found in his experiments to Bertalanffy's theory."
The relations found are summarized in table 4, which indicates the metabolic types, the corresponding growth types, and examples investigated. It is hoped that these investigations will lead to a comparative physiology of metabolism and growth.

<table>
<thead>
<tr>
<th>Metabolic type</th>
<th>Growth type</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>I. Respiration surface-proportional</td>
<td>(a) Linear growth curve: attaining without inflexion a steady state.</td>
<td>Lamellibranchs, fish, mammals</td>
</tr>
<tr>
<td></td>
<td>(b) Weight growth curve: <em>sigmoid</em>, attaining, with inflexion at c. ( \frac{1}{3} ) of final weight, a steady state</td>
<td></td>
</tr>
<tr>
<td>II. Respiration weight-proportional</td>
<td>Linear and weight growth curves <em>exponential</em>, no steady state attained, but growth intercepted by metamorphosis or seasonal cycles</td>
<td>Insect larvae, Orthoptera, Helicidae</td>
</tr>
<tr>
<td>III. Respiration intermediate between surface- and weight-proportionality</td>
<td>(a) Linear growth curve: attaining with inflexion a steady state.</td>
<td>Planorbidae</td>
</tr>
<tr>
<td></td>
<td>(b) Weight growth curve: <em>sigmoid</em>, similar to I(b)</td>
<td></td>
</tr>
</tbody>
</table>

LITERATURE CITED


1943b, Ibid. IX: Der Zusammenhang zwischen Koerpergroesse und Stoffwechsel bei *Dixippus morosus* und seine Beziehung zum Wachstum. Z. vgl. Physiol. 30: 130.
Unpublished.


